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Soil Biodiversity and Root Pathogens in Agroecosystems

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Abstract

Soil ecosystem is a living and dynamic environment, habitat of thousands of microbial species, animal organisms and plant roots, integrated all of them in the food webs, and performing vital functions like organic matter decomposition and nutrient cycling; soil is also where plant roots productivity represent the main and first trophic level (producers), the beginning of the soil food web and of thousands of biological interactions. Agroecosystems are modified ecosystems by man in which plant, animal and microorganisms biodiversity has been altered, and sometimes decreased to a minimum number of species. Plant diseases, including root diseases caused by soil-borne plant pathogens are important threats to crop yield and they causes relevant economic losses. Soil-borne plant pathogens and the diseases they produce can cause huge losses and even social and environmental changes, for instance the Irish famine caused by *Phytophthora infestans* (1845–1853), or the harmful ecological alterations in the jarrah forests of Western Australia affected by *Phytophthora cinnamomi* in the last 100 years. How can a root pathogen species increase its populations densities at epidemic levels? In wild ecosystems usually we expect the soil biodiversity (microbiome, nematodes, mycorrhiza, protozoa, worms, etc.) through the trophic webs and different interactions between soil species, are going to regulate each other and the pathogens populations, avoiding disease outbreaks. In agroecosystems where plant diseases and epidemics are frequent and destructive, soil-borne plant pathogens has been managed applying different strategies: chemical, cultural, biological agents and others; however so far, there is not enough knowledge about how important is soil biodiversity, mainly microbiome diversity and soil food webs structure and function in the management of root pathogens, in root and plant health, in healthy food production, and maybe more relevant in the conservation of soil as a natural resource and derived from it, the ecosystem services important for life in our planet.

Keywords: soil biodiversity, soilborne plant pathogens, soil food webs, ecological interactions, plant pathogens management

1. Introduction

Soil ecosystem is a living and dynamic environment, habitat of thousands of microbial species, animal organisms and plant roots, integrated all of them in the food webs, and performing vital functions like organic matter decomposition, nutrient cycling and release, promote plant growth, receive, hold and release water, transfer energy in the detritus food chain, and act as an environmental buffer [1–3]; soil is also where plant roots productivity represent the main and first

trophic level (producers) [4], the beginning of the soil food web and of thousands of biological interactions [5, 6]. In Agroecosystems, the different activities practiced by man will affect all the biological processes carried out above- and belowground, including soil biodiversity and soil food webs [7], depending of the kind of agroecosystem (traditional or intensive), the geographical region, the crop management, and social and economic interests. Human societies have developed several kinds of agroecosystems, from traditional/subsistence, multicropping, to intensive and highly technified crops [8–10] however, plant pathogens and pest diseases are a common component of the agroecosystem, and by some degree all of them are affected [11]. In this sense, a relevant and unavoidable problem is the soil degradation and contamination in agroecosystems; plant diseases caused by soilborne plant pathogens (SBPP) are of great importance because most of the strategies applied for their control are directed to the soil [12]. Management of SBPP and diseases require a broader view and a thorough ecological knowledge of the soil ecosystem, considering the improvement and conservation of the soil biodiversity and the soil food web structure and function, and studying the soil as a dynamic ecosystem in time and space. Plant pathologist and agronomist must know about the importance of the soil ecosystem, its biodiversity, the different and multiple functions soil organisms perform, how every and all soil organisms are connected through different relationships established as a result of natural selection forces, and how they have evolved throughout the time [13, 14]. And maybe most important is to understand how a disturbance or stress factor imposed on soil organisms may have a cascade effect in the whole processes and functions of the soil ecosystem. In this work we are talking about the biological soil diversity and functions, the soil food web, the ecological interactions among species and how they are important in the management of root pathogens and the diseases they cause. It seems there is an urgent need for redesigning and developing sustainable agroecosystems where soilborne plant diseases and pathogens be analyzed under an integral knowledge with the application of plant pathology, plant disease epidemiology, and ecological and evolutionary principles [15]. Even more if the agroecosystems of interest involve soilborne plant pathogens and diseases, studies must comprehend the important role that soil biodiversity [16] and its multiple interactions and relationships play in the regulation of the SBPP, and how this regulation is expressed through the soil food web (structure and function) and through other complementary relationships.

2. Soil biodiversity

The soil is an ecosystem, a living system where interplay mineral and organic materials. Soils are built up through millions of years, from the parent rock layer to the small sand, lime and clay particles derived from physical and chemical intemperization processes, and from biological activities which perhaps be the most important factor in the soils formation. Of the total soil components, organic material represents 5 to 10%, from this percentage 10 to 20% is the active fraction, from the active organic fraction only 20 to 40% are living organisms, and from these 50% are fungi, 30% are bacteria and actinomycetes, 10% are yeasts, algae, protozoa, and nematodes, and 10% are fauna. This means, the active microbial biomass represents 90% of the soil living organisms. Another essential component in soil biodiversity is the soil fauna which is divided in function of their size (mm) into micro-, meso- and macrofauna. Microfauna includes Protozoa, Rotifers from 0.005 to 0.2 mm; mesofauna is composed by nematodes, arthropods, enchytraeids, mites, springtails from 0.2 to 10 mm; macrofauna include animals like insects from 10 to 20 mm; and

megafauna includes earthworm (≥ 20 mm), macroarthropods and small mammals (cm) [2, 3, 17, 18].

Plant roots are another fundamental component of the soil biodiversity, they represent the primary source of organic matter in soil, and the amount of root production is relevant in the process of decomposition and cycling into organic matter in soils. Roots are the subterranean organ of the plant, and they fix them to the soil. Plants take water and nutrients from soil through the roots and the root vascular system transport them to the upper parts of the plant; in some cases, roots are a storage organ [19]. Root exudates and rhizosphere are relevant components for root functioning, and they are essential for all the biological and soil microbial activities like attraction of mutualist symbionts and pathogenic microbes, release and cycling of nutrients, allelopathic processes [5, 6] and also for physical and chemical soil characteristics such as soil aggregation and structure, cation exchange capacity and pH [20]. Plant roots represent the first trophic level (autotrophs entities) in the soil trophic web, from which microbes and small fauna obtain their nutrients and energy [18].

Soil-borne plant pathogens (SBPP) are a component of the soil ecosystem, and also members of the soil biodiversity; these microorganisms live part of their life in soil and in the plant rhizosphere, but they also infect and damage the plant roots from which they feed; in some way plant roots are their habitat. SBPP include organisms from bacteria, fungi, oomycetes, nematode, protozoa groups and meso-biotic entities like virus and viroids [11, 21].

3. Importance and function of soil biodiversity ¿who are here and what they do?

3.1 Bacteria and fungi

Bacteria and fungi participate in the rock intemperization (degradation) through their biochemical enzymatic activity; these microorganisms initiate the soil formation, and with it the important process of mineral transformation and nutrient liberation [22]. As soil is formed and deeper, it is possible for other microorganisms and larger organisms like protozoa, rotifers, nematodes, worms, small arthropods, and also spores of bryophytes, moss, ferns, and mycorrhizal fungi to arrive and to establish. When soil has enough deep and biological activity is adequate for higher plant seeds to germinate and their root systems to interact with the soil microbiome, it begins the formation of a plant community and in time, with the integration of higher animals and through a successional process, the establishment of a biome after hundreds and millions of years.

3.2 Soil bacteria

Certain groups of the soil bacteria community participates in the N cycle which involve four stages or reactions: a) Nitrogen fixation carried out by nitrogen-fixing bacteria (e.g. *Rhizobium*, *Azotobacter*, *Bradyrhizobium*), b) Ammonification performed by ammonifying bacteria or decomposers bacteria (*Bacillus subtilis*, *Pseudomonas fluorescens*), c) Nitrification accomplished by nitrifying bacteria (e.g. *Nitrosomonas*: NO_2 nitrite, *Nitrobacter*: NO_3 nitrate), and d) Denitrification realized by denitrifying bacteria (some species of *Serratia* and *Pseudomonas*) [23, 24]. It must be noted that bacteria also participate in the C biogeochemical cycle, and they play a crucial role in the regulation of C and N cycles during biological soil crust succession in arid and semi-arid ecosystems [24]. It is important to indicate

that some of these bacteria species besides to participate in the Nitrogen cycle, like *Bacillus subtilis*, *B. amyloliquefasciens*, *Bradyrhizobium* (Nod Factors), they also are involved in a complex network of signaling pathways mediated by plant hormones like jasmonic acid, ethylene and salicylic acid and in the release of volatile organic compounds which trigger the induced systemic resistance (ISR) and the acquired systemic resistance (ASR) in plants, in response to the presence of both beneficial microbes and plant pathogens invasion and infection, and also to insect attack [25–30]. Some bacteria specific strains also produce different antibiotics, e.g., *Pseudomonas fluorescens* F113 produces 2,4-diacetyl-phloroglucinol against *Pythium* spp. [31], *Bacillus amyloliquefasciens* FZB42 produces bacillomycin and fengycin against *Fusarium oxysporum* [32]; enzymes, and siderophores e.g., *Pseudomonas putida* WCS358 against *Pseudomonas syringae* pv. tomato and *Fusarium oxysporum* f. sp. *raphani* [33], which are important components in their performance as biological control agents against plant pathogens [7, 34]. Another important activity performed by some soil bacteria is enhancing the plant growth through the production of growth regulators (hormones) like auxins (Indol Acetic Acid, IAA), cytokinins, gibberellins, or ethylene, and these bacteria are known as Plant-Growth Promoting Bacteria (PGPB) [35]; examples of bacteria species involved in this activity are *Pseudomonas fluorescens*, *P. putida*, *P. gladioli*, *Bacillus subtilis*, *B. cereus*, *B. circulans*, and bacteria in the genre *Azospirillum*, *Serratia*, *Flavobacterium*, *Alcaligenes*, *Klebsiella* and *Enterobacter* [7].

3.3 Soil fungi

Fungi, organisms in the Kingdom Fungi, perform different and important functions in soils, they are organic matter decomposers due to their great ability to degrade complex substrates of plant origin [36]. Fungi participate in the mineral degradation and in the release and cycling of nutrients; they are also involved in the C and N cycling [24, 36, 37]. These microorganisms are vital for soil functioning because most carbon in our planet is stored in rocks and sediments [38]. They also contribute to the soil particles aggregation and soil structure because of their filamentous form and exudates [39]. In soils exist a complex and diverse fungal community widely distributed [40]. This fungal community is composed by different and important functional groups. One of the most studied is the mycorrhizal fungi, which exists as mutualist symbionts in most of the plant species in natural ecosystems and it has a long evolutionary history [41, 42]; some of them develop a net of hyphae external to the roots and growing intercellularly in the root cortex, they are ectomycorrhiza; but other mycorrhiza can penetrate the roots and establish intracellularly in the cortex cells forming small structures called arbuscules, they are named arbuscular mycorrhiza or endomycorrhiza. Both kind of mycorrhiza help the plant host in the uptake of nutrients from soil and protection against pathogens. Arbuscular mycorrhizae play a central role in the Phosphorus cycle, but they are equally important in the Nitrogen cycle [43, 44]. Mycorrhiza hyphae link the plants roots with the soil particles, interconnect directly the root systems of two different individual plants, and they also interact with different kind of soil microbes (synergistic and antagonistic); even more, there is evidence of the extra radical mycorrhizal hyphae associated with symbiont bacteria (hyper symbionts) for acquisition of C [45]; therefore, ecto and endomycorrhizae fungi play important functions in the physiology, ecology and evolution of their host plants.

Fungal Endophytes are other important functional group of fungi, and they enter and live inside the plants [25, 42]. Here, endophytes are defined as those microorganisms (bacteria, fungi, virus) which live their life cycle or part of it inside a plant, within asymptomatic tissues, performing and promoting a beneficial functioning in

the plant host, and enhancing its fitness in plant communities by conferring abiotic and biotic stress tolerance; therefore, this relationship has ecological and evolutionary importance [42, 46, 47]. Endophyte organisms can be found in different plant organs like roots, stems, leaves, reproductive organs (e.g., vanilla flower ovaries) and fruits (e.g., vanilla pods) [42, 48]. Endophytic fungi participate in different plant functions, some of them enhance plant growth and nutrition and are referred as Plant-Growth Promoting Fungi (PGPF) [25], and they also strengthen plant defense against pathogens and insects below- and above-ground [46, 47]. Endophyte fungi control plant pathogens attack through different processes: niche exclusion, antibiosis, predation, mycoparasitism and ISR induction [25]; it is also possible to find hypovirulent pathogen isolates which will control more virulent isolates as happens with *Monosporascus cannonballus* against monosporascus root rot vine decline [49], or with *Fusarium oxysporum* strain Fo47 [50, 51]. Endophyte fungi can express simultaneously more than one control mechanism against plant pathogens as it was showed with *Trichoderma* isolates that besides attack directly *Botrytis cinerea*, also induced systemic resistance to this pathogen [52]. Other fungal endophytes additionally of increasing plant biomass, confer drought tolerance, and produce chemicals that are toxic to animals like insects [46, 47], birds and small mammals and decrease herbivory [53]. Certain endophytic fungi have an important role in physiological and biochemical aspects during development of flower and chemical compounds, as is the case of *Vanilla planifolia* compound vanillin [48]; researchers have found that fungal endophytes inoculum from soil get into the roots through rhizosphere, but other endophytes come from the fungal airborne inoculum and enter into the flower ovaries, and later in the vanilla pods, participating in the vanillin process and therefore in the vanilla flavor [48]. Endophyte fungi described as PGPF include important genera like *Fusarium*, *Trichoderma*, *Aspergillus*, *Penicillium*, *Colletotrichum*, *Cylindrocladium*, and others; some of them are nonpathogenic or hypovirulent strains of plant pathogenic fungi [25, 42].

Some soil fungi are pathogens of other microorganisms like bacteria [54], fungi and nematodes [55], plants [11], insects and arthropods [47]; for instance, *Metarhizium anisopliae* and *Beauveria bassiana* are endophytic and pathogenic in insects, while *Paecilomyces lilacinus* is endophytic and pathogenic in nematodes [55]; these fungi take part in the regulation of their hosts populations and they are of relevance in the biological control and management of agroecosystems [46]. As mentioned above soil fungi are included in several functional groups: decomposers, mutualists (mycorrhiza), endophytes, pathogens, parasites, and every one of these activities are of great relevance for the soil ecosystem function.

3.4 Soil virus

Viruses are considered entities between living and non-living state, quasi-organisms; they are composed by RNA or DNA molecules contained within protein capsids, and they are mainly known as pathogens in plants, animal, and the human being, causing important diseases. However, and fortunately, with the help of the molecular biology methods, in the last 10 years there has been an unprecedented interest and research about virus diversity and functions in different environments: marine and soils [56, 57]. Knowledge about soil viruses are just beginning, very little is known about their ecology in soils [2, 56, 58]. However, it is suggested they participate in the biogeochemical cycling of Carbon [59], as well as in short-term adaptation and long-term evolution of microbes [2], through their infection like bacteriophage on beneficial bacteria (Rhizobia) and soilborne plant pathogens (bacteria, fungi, virus, nematodes and other soil organisms) [56]; they also perform horizontal gene transfer (transduction) among bacteria

[60]. Viruses impact the evolution and ecology of their plant hosts, and they seem to have a mutualistic relationship rather than a pathogenic one under experimental laboratory conditions [57]. On the other hand, plant pathogen viruses cause great economic and yield losses in agroecosystems where they are vectored by insects (aphids, white flies, trips, etc.), but they also are transmitted by mechanical ways. There are just few soilborne plant pathogenic viruses known so far, and they are transmitted by fungi and nematodes [61, 62].

3.5 Soil protozoa

Protozoa are other important component in the soil ecosystem and in the food web. The free-living protozoa feed from microbes like bacteria and fungi (non-pathogenic and pathogenic) [63], and also from algae; they are included in four groups: flagellates, naked amoebae, testacea amoebae and ciliates. They contribute to the regulation of these microbes population densities and dynamic. Protozoa also play an important role in the nutrient turnover [64].

3.6 Soil nematodes

Soil nematodes are some of the most abundant invertebrate animals in soils, they often reach densities of 1 million/m²; they are worm-like microorganisms and live in water films or water-filled pore spaces in soils [64]. Many kinds of nematodes are found in the rhizosphere of roots and root hairs because of the rich exudates. They help to accelerate organic matter decomposition when they graze on bacteria, fungi, and plant residues [18]. Nematodes biological characteristics like structure, physiology, diverse reproductive patterns, and adaptability help them to inhabit many and different environments [65].

3.7 Earthworms

Earthworms participate in the fragmentation, breakdown, and incorporation of the soil organic matter, affecting its physical and chemical characteristics, and in turn other soil biota organisms [2]. They also affect positively soil structure helping in pores formation and particles aggregation, contributing to the soil aeration and better water distribution. Earthworms play an important role in C and N cycling [66]. Ecologically, earthworms promote diversity of fungal species and oribatid mites through their casts from where they feed, and through reducing competition between fungal species [67].

3.8 Soil arthropods

Arthropods in soil, are other important component in soil biodiversity. After microbes and Protozoa, microarthropods play a very important role in soil activities, they participate in the organic soil matter decomposition, nutrient release and cycling, but they also enhance plant growth and the expression of induced systemic resistance to pests in plants [68]; participate in the secondary seed dispersal of higher plants and dispersal of sperm in lower plants like mosses [69]; they are involved in the regulations of population densities of bacteria and fungi including plant pathogenic organisms and decomposition of agrochemicals [17, 70]. Microarthropods like collembola, protura, diplura, isopoda and others are also components in the soil food web, and they have been included as indicators of soil health and soil disturbance because they live a sedentary life and express the habitat conditions better than those organisms with a high dispersal capacity [18, 71, 72].

3.9 Soil-borne plant pathogens (SBPP)

Different groups of soil microorganisms bacteria, fungi, nematodes, protozoa and entities like virus and viroids may also act as plant root pathogens, and they received the name of soil-borne plant pathogens. These plant pathogens damage all kind of plants in the different botanical taxa in both natural and worldwide managed ecosystems; however, in agroecosystems their damages have economical relevance due to the resulted crop yield losses [73, 74]. However, SBPP like other plant pathogens play important roles in the structure, function, and diversity of natural plant communities [75–78]; they also are important in the evolution of the plant host-pathogen relationship [13, 79].

We can see, microorganisms have developed multiple, diverse and vital relationships through time and space with all other organisms in the soil ecosystem including plant roots, insects, and animals, and maybe most of these relationships have been developed in response to nature selection forces throughout an evolutionary time. It is necessary to mention that soil type [80] and soil management [81] have an important influence on the diversity and structure of soil microbial diversity, and in other soil microorganisms such as protozoa, rotifers, nematodes, microarthropods, mites, and of course in worms, ants, termites and small mammals [18]. However, plant roots, the principal C source in soils, and their rhizosphere exudates determine in relevant way, the spatial structure and diversity of the soil microbial and microorganisms community [82].

4. Trophic webs and complementary or interference interactions in soil “not everything in life is food”

Since the beginning of soil formation from the parental rock, biological activity is fundamental, many biological interactions are established, and they initiate the soil trophic web. At the beginning, trophic webs may be simple and with few components, but as root biomass and their exudates increase in amount and different types, the soil trophic webs are more complex in their biological diversity, structure and functions. Plant roots are key components in soil function, they provide most of the organic matter to the soils [4], they are the first trophic level in the soil food web and represent the autotroph organisms (photosynthesizers) from which heterotrophs organisms in the next trophic levels obtain their food and energy [83]. Plant roots and specifically the rhizosphere region have a transcendental role in the dynamic of soil microbial activities through the development and release of rhizodeposits [6, 84]. Rhizodeposits include sloughed-off root cap and border cells, mucilage, and exudates. The exudates are made up of organic acids, amino acids, proteins, fatty acids, enzymes, sugars, phenolic metabolites and other metabolites which are used by microorganisms [84, 85]. Most of the root exudates are released at the root cap and the meristematic zone behind the root cap; therefore, these regions are considered important for determining the temporal and spatial activity and distribution of the microbial communities [82, 84, 85].

Bacteria and fungi together with protozoa, plant pathogenic nematodes and fungi, are in the second trophic level of the soil food web, they are heterotrophs and they may function as decomposers, mutualists, pathogens, parasites and root-feeders, and they are food for the third trophic level (heterotrophs) that includes also nematodes and protozoa (bacterivorous and fungivorous), and microarthropods which work as shredders, predators and grazers; organisms from this level are food for the fourth and fifth trophic levels (heterotrophs) which include higher level predators like arthropods, small mammals, birds [83].

Soil protozoa is a group of microorganisms which has not been studied so deep and frequently like bacteria or fungi, and their role in the soil food web is sometimes considered only like predators and grazers of microbes; however, they interact with the root systems and bacteria in several and particularly important modes. Bonkowski and Brandt [86] worked with an Amoebae, specifically with *Acanthamoebae* sp. which is considered the most common soil free-living protozoon, and they found this amoebae have a positive effect on root elongation and branching in interaction with rhizobacteria, and mention that “Protozoa function as bacteria-mediated mutualists promoting plant growth by hormonal feed-back mechanisms and nutrient effects based on nutrient release from grazed bacterial biomass”; these bacteria may also be involved in the different phases of the soil nitrogen cycle. All these activities occur in the soil microbial loop [87], as a relevant component of the soil food web.

Soil nematodes are considered important component in the soil food web; their soil communities are usually large and species-rich, with different functional groups (bacterivores, fungivores, herbivores, omnivores, predators, parasites and pathogens), located in different trophic levels: root feeders nematodes in second trophic level (decomposers), fungi and bacterial feeder nematodes in third trophic level (grazers), nematode and protozoa predators in fourth trophic level (higher level predators), in this way nematodes participate in the regulation of soil microbial communities and indirectly in the flux of plant nutrients. Because of their biological characteristics (they are ubiquitous, abundant and diverse), they respond soon to changes in the soil environment, and for this reason they have been considered as important indicators of the soil health [18, 70, 88, 89].

Plant pathogens and therefore soilborne plant pathogens are also an important component inside the soil food web and the ecosystems [90, 91]. They can be considered as microherbivores because they feed over root systems, and later they are food for the next trophic level, protozoa, nematode, rotifers, mites, and microarthropods.

4.1 Plant root diversity and their effects in soil diversity and soil food web

Plant roots are the principal biomass and C source in soils; as roots and their exudates grow, they die and are decomposed by soil microorganisms and incorporated into the soil organic matter [4]. Plant roots are of many different types, lengths and architecture with a main and secondary roots and root hairs [92]. Roots produce different kind of exudates, and this is influenced by the plant species, soil physical and chemical conditions, soil temperature and moisture [82, 93]; however, root exudates are also affected by the rhizosphere microbial community [82]. Root exudates supply nutrients, they prevent invasion by other plant species (allelopathy), they function also like especially important chemical signals for attracting symbionts (chemotaxis) e.g., rhizobia and legume, and other beneficial organisms as plant-growth promoter bacteria and fungi [94–96]. With all the diversity of plant roots, exudates, microbes, and other soil organisms it is expected that in soil occur different interactions and responses which will be reflected in the soil food web structure, diversity, and function [87].

Complexity of soil food web involves the species number and the number of different kind of species (trophic and functional groups); other characteristics as connectedness, interactions strength and length of chains are important in the food web stability [97]. Throughout the soil food web the main relationship is the vital need to obtain food and energy to accomplish the life functions and the species survival; however this relationship acquire different tonalities when each microbe or protozoa; or arthropod species in the soil, develops different life strategies in response to specific

natural selection forces, and they establish inter- and intraspecific biological interactions like mutualism, competition, parasitism, predation, pathogenism, fungistasis, antibiosis, allelopathy, herbivory. These ‘complementary’ interactions among species are of ecological relevance because throughout them is built up the structure, function and diversity of the soil community; Wardle [67], talks about some of these kind of interactions as ‘interference interactions’ and he indicates that apply primarily to interactions among fungi, among bacteria, and between bacteria and fungi.

Microbial symbionts (endosymbionts) play vital roles inside plants, fungi, nematodes, protozoa, insects (termites, ants), etc. [45, 98–100]; they are interactions inside interactions and are “*complementary interactions*” that biological species have been developed and evolved throughout time and space, improving their fitness [25, 45, 56]; without them the host species would be unable to live. All kind of symbionts are also components in the soil food web; some of these relationships are obligate or facultative, and others are intermediate between an obligate and facultative behavior, depending on the press of natural selection forces and the evolutionary time through which these species have been related [101]. What about the role pathogens play in the soil food-web, and the role plant pathogens have in different important functions for plant life: seed germination [77], seedlings and young plant establishment [76], plant sexual reproduction and sexuality expression [102, 103] and their role in plant community successional process? Ecological functions of pathogens and specifically of plant pathogens, have received few attention in the plant communities of wild ecosystems [104–106], even though Dinor and Eshed [105] drew the attention about the importance of studying plant pathogens and disease they cause in natural ecosystems, to better understand plant diseases in agroecosystems and applied the best management strategies.

To this point, we have seen that soil organisms play multiple and different activities in the soil ecosystem and all of them are relevant for the soil dynamic functioning (**Table 1**); in fact, the FAO Report of 2020 talks about “The Multifunctionality of Soil Biodiversity” [107]. But what drives soil microbial diversity? Soil ecologists suggest that innate soil spatial heterogeneity, or patchiness, would be a main environmental factor to explain soil biodiversity at different spatial and temporal scales, arguing that soil heterogeneity ‘*provides unrivaled potential for niche partitioning, or resource and habitat specialization, leading to avoidance of competition and hence co-existence of species*’ [1]. At the same time, the knowledge of the multiple and diverse biological intra- and interspecies interactions that happen in the soil environment at all levels of biological organization, and taking as a fundamental basis the structure and complexity of the soil food web, we reason that these two factors: soil spatial heterogeneity and ecological interactions (trophic and complementary interactions) working together through evolutionary processes and time, at the population and community levels, have resulted in the immense soil biodiversity.

Pathogens affect all groups of organisms: plants, microbes, protozoa, nematodes, insects, etc.

Food webs, and therefore soil food webs, are biological systems organized with different subsystems (trophic levels), and sub-subsystems (functional groups in each trophic level). Food webs are also open systems, with a spatio-temporal dynamic of the whole, in which each subsystem and each subsystem component has also its own dynamic function but interrelated with other components in the web-system. Food webs are open systems with energy and material flow, and in some cases there is also a flow of genetic information (e.g., fungi endophytes maybe transmitted through vertical or horizontal gene transfer, [47]). In this sense, ecologists have mentioned that “*The analysis of energy and material flow is considered to be fundamental to understanding the patterns and dynamics in ecosystems and the way ecosystems are organized.*” [97].

Trophic level		Producers	Consumers (first level)		Predators (first level)		Predators (second level)		Higher Predators	Ecosystem Services performed by Soil Biodiversity at the Community Level
Biological Organization Level	Activity	Plant Roots	Bacteria	Fungi	Protozoa	Nematodes	Micro Arthropods	Earthworms	Insects, Birds, Small Mammals	
INDIVIDUAL	Root Biomass Productivity and release of Root Exudates	✓								
	Organic Matter Decomposition		✓	✓						
	Mineralization (N, P, C)		✓	✓						
	Nutrient Cycling		✓	✓	✓	✓				
	Induction of Plant Resistance (ISR, AR)		✓	✓	✓	✓				
	Signaling Pathway in Plant Growth Promotion		✓	✓	✓	✓				
	Development of toxins against herbivores			✓						
	Abiotic Stress Tolerance		✓	✓						
	Enhancement of Plant Fitness		✓	✓						
POPULATION	Regulation of Population Densities		✓	✓	✓	✓	✓	✓	✓	Water Reservoir ↓ Weather Buffering ↓ Soil Health ↓ Healthy Plants ↓ Oxygen Release ↓ Disease Suppression ↓ Soil Conservation ↓ Climate Regulation
	Regulation of Populations Dispersal and Spatial Pattern			✓	✓	✓	✓	✓	✓	
COMMUNITY	Enhancement of Physical and Chemical Soil Environment (soil structure, aeration and water movement and holding capacity)					✓	✓	✓	✓	
	Influence in the dispersal and spatial pattern of plant species in a community		✓	✓	✓	✓	✓	✓	✓	
Pathogens affect all groups of organisms: plants, microbes, protozoa, nematodes, insects, birds, mammals, etc., in different life-strategies and processes, e.g., seed germination, seedling establishment, plant sexual reproduction, sexuality expression, successional process, impaired competition.										

✓ = Indicates participation in the activity

Table 1. Multiple and different functions performed by the soil organisms at the individual, population and community organization levels in the soil ecosystem and soil food web, considering the ecosystem services.

With all the information presented here, it is argued that most of the trophic relationships in the soil trophic web has been established through evolutionary processes, and this is an important basis to understand that disturbances (e.g., plant disease epidemics) in the soil food web can have irreparable consequences in the ecosystem functions, e.g., natural or managed systems. Disturbances that occur in the soil environment will cause changes at different physical and biological levels; these perturbations will affect the ecological interactions and depending on the strength and duration of the perturbation, soil ecosystem will be able to recover through its resilience and resistance capacities, expressed at the individual (e.g., dormancy), population (temporal and spatial population density and dynamics) and community (regulation throughout mutualistic vs. antagonistic relations) levels [108]. These processes will be evidenced in the complexity of the structure and diversity [108, 109] and in the stability of the soil food web [97]; However, we must also keep in mind that all the multiple and different soil organisms since plant roots to microorganisms and to animals, all together as a whole, participate in vital soil processes such as biogeochemical and nutrients cycling, soil formation and conservation, and climate regulation [2] (Table 1). In this sense De

Ruiter and Moore [110], indicated that 'soil food webs are thought to govern major components in the global cycling of materials, energy and nutrients'.

Soil ecologists indicate that soil food web complexity improves the turnover of nutrients, enhance soil structure, water holding capacity and infiltration, promotes disease suppressiveness, pollutants degradation and biodiversity [18, 110]. All the different interactions that soil fungi and bacteria have established with other soil microorganisms like protozoa, nematodes, rotifers, microarthropods, mites, ants, and root plants, establish the foundations for a complex soil food web with direct and indirect biological and ecological relationships. Complexity and performance of the soil food web is also affected by physical and chemical soil factors; soil structure, particles aggregation, pore size [111], soil texture, pH [22], amount of organic matter, all of them affect direct and indirectly the soil biological species diversity, their interactions, their population densities and their spatio-temporal dynamics. At the same time, every biological activity performed by the soil community will transcend and affect some physical and chemical characteristics in soil. It is important to mention that trophic and non-trophic relationships in the soil community and ecosystems have been developed through time and they are ruled by natural selection forces, which mean, trophic food webs have evolutionary and ecological basis [101].

5. Root pathogens: soil borne plant pathogens

Soil Borne Plant Pathogens include organisms from bacteria, fungi, oomycetes, nematode, protozoa groups and mesobiotic entities like virus and viroids [11, 73, 112]. SBPP penetrate, infect and invade the roots using different biochemical and physical mechanisms, causing cell and tissue damages; they feed and establish at different regions in the roots including xylem and phloem, but they also obtain their food and energy from rhizosphere root exudates. SBPP are endo-, ecto-, or semi-endo-pathogens what means they can enter and live their whole life cycle inside roots, or they live some life stages in the soil. In plant pathogenic nematodes, there are species in which young and immature females penetrate only half of their body into the epidermal and cortex cells in the roots (*Tylenchulus semipenetrans*), until they mature and transform into a swollen body containing eggs that are released into the soil (*Meloidogyne* sp.); some plant nematodes are sedentary (*Xiphinema* sp.) while others migrate inside the roots (*Pratylenchus* sp., *Radophulus* sp.) or go up to the stem (*Ditylenchus* sp.) [11, 113]. Soil borne plant pathogens produce localized or systemic damages; they damage the roots producing root rots, wilts, necrosis and death [114] which impair nutrients and water uptake to the upper plant organs, where damage is manifested as seedlings damping-off, stunt, chlorosis, wilts, bark cracking, twigs and branch diebacks, drop of flowers and fruits, and in consequence biological and economical yield losses [12, 112, 115–117]. SBPP are obligate or facultative pathogens; some of these pathogens may live also as soil saprophytic organisms depending on substrate availability and soil environmental conditions. When soil environment conditions are adverse, many SBPP develop resistance structures (e.g., sclerotia, cysts, oospores, chlamydospores), and they enter in a dormancy stage for until 20 (*Sclerotium cepivorum*) or 30 years (*Rhizoctonia solani*) [11, 73, 118].

SBPP produce different kinds of propagules, which refers to any entity or unit able to multiple, disperse and conserve the pathogen population, e.g., in fungi: spores, conidia, sporangia, sclerotia; in nematode: eggs, cysts, immature stages, adult male and female; in virus: they are vectored by fungi, nematodes and mites [11]. Propagules and resistance structures of SBPP remain in soil as inoculum that is dispersed by water, microfauna, and cultural practices. There are important and

unique pathogen traits which contribute to their successful establishment, increase and eventual epidemic expression, and these are inoculum density, pathogenicity, virulence, dispersal ability, reproductive mode (sexual/asexual), secondary hosts, and long-term resistance and survival structures in soils [12, 119]. SBPP are another natural component of the soil communities and part of the soil food web, they interact with plant roots, but they also interact with other soil organisms in mutualist and antagonist relationships [78, 120], and all these interactions shape the SBPP population density and dynamics in time and space. Some examples of important SBPP affecting plant communities and crops are, fungi: *Fusarium oxysporum*, *Rhizoctonia solani*, *Verticillium dahliae*, *Armillaria mellea*, *Gaeumannomyces graminis*, *Sclerotium cepivorum*; Oomycetes: *Phytophthora cinnamomi*, *P. capsici*, *Pythium aphanidermatum*; nematodes: *Meloidogyne incognita*, *Nacobbus aberrans*; bacteria: *Ralstonia solanacearum*, *Agrobacterium tumefaciens*; mesobiotic entities: lettuce necrotic stunt virus (LNSV), spindle tuber of potato viroid. Economic and yield crop losses caused by SBPP diseases are significant and may provoke loss of the total crop yield as in the white root rot of onion and garlic caused by the fungus *Sclerotium cepivorum* when inoculum density is high and persists in soil for long time [117].

5.1 Function of root pathogens

Plant (Root) pathogens has also been considered as microherbivores [91], which in the process of feeding from plants they release different enzymes (cellulases, chitinases) and develop different structures (fungi: haustorium, appressorium) or used structures like the nematodes stylet to enter de (root) plant tissues; at the same time, they also elicit defense/resistance mechanisms by the host plant. Plant pathogens are important components in different ecological processes of the plant community like structure and succession, development (expression) of sexuality, seed germination and establishment of seedlings [76, 105, 121–123], competition between plant species [77] and expression of allelopathy [124]. Since an evolutionary point of view, plant pathogens are important drivers of evolution of both species, the host plant and pathogen [13, 106], and therefore in the diversity of the two species involved in the process of pathogenicity [78, 125, 126].

5.2 Diseases caused by root pathogens in wild ecosystems

We know SBPP are natural components in wild ecosystems and they participate in important ecological and evolutionary processes in plant communities; however they may also cause severe and destructive epidemic diseases in nature system, as it happens in Jarrah (*Eucalyptus marginata*) forests in Western Australia which have been devastated during the last 100 years by the dieback disease epidemics caused by the Oomycete *Phytophthora cinnamomi* Rands, an exotic root pathogen introduced into Australia in the XIX century, with a host range over than 2000 plant species in more than 48 botanic families [127–129]. The destructive effect of this SBPP has caused cascade negative effects on the Australian forest ecosystem because affects indirectly, different species of insects, birds and small mammals who use to feed on the plant species destroyed by *P. cinnamomi* [130]. Dieback disease epidemic have destroyed large areas of the jarrah forest to the point that they are known as black gravel or graveyard sites because these sites are devoid of the plants and animals they supported [131]; this epidemic disease has disrupted the aboveground food web, and certainly the belowground soil food web. Plant disease epidemics caused by SBPP in wild ecosystems are uncommon so far, but they may be quite destructive, threatening entire plant communities and ecosystems [130].

6. Resilience in soils

Belowground roots, exudates, microbial and microorganisms diversity conform a complex and diverse soil food web with multiple trophic and complementary relationships, which can be classified as mutualists (+) and antagonists (–) relationships that in theory must result in a well-balanced soil system where is expressed the suppressiveness to SBPP; these are called “suppressive soils”. In the development of the biological control of SBPP the concept of suppressive soils has been a key one, because take in consideration that in the soil ecosystem there are a whole microbial (fungi and bacteria) community with the potential to interact with root pathogens and regulate their population densities and dynamic under certain physical and chemical soil environmental conditions. Baker and Cook [21] originally defined suppressive soils as “soils in which the pathogen is not able to establish or persist, the pathogen establishes but causes no damage, or the pathogen causes some damage, but the disease becomes progressively less severe, even though the pathogen persists in soil”. Development of molecular biology methodologies has allowed to better understand that in the soil microbial community, certain groups of bacteria and fungi are involved in soil suppressiveness. Mendes et al. [132] found thousands of bacteria and archaeal species in the groups of Proteobacteria, Firmicutes and Actinobacteria constantly associated with suppression to disease caused by *Rhizoctonia solani* in beet. In other research Penton et al. [133], resolving soil disease suppression to *R. solani* strain AG8 and *Fusarium pseudograminearum* in cereal fields in Australia, found that suppressive soils were attributed to less than 40 genera of fungi, including certain endophytic species and mycoparasites in the groups Ascomycota, Basidiomycota and Chytridiomycota; the fungi genera most associated with the suppressive fields were *Xylaria* (endophyte), *Bionectria* (mycoparasite), *Anthostomella* (saprotrophic), and also with antifungal activity *Chaetomium*, *Corynascus* and *Microdiplodia*; these authors indicate the importance of analyzing soil suppressiveness including both fungi and bacteria, and their interactions with fungi and plants. It has been mentioned that ecosystems as open systems, have the ability of buffering negative stresses throughout their resilience and resistance properties expressed at the population, community, and ecosystem levels [108], but this ability depends on the strength and time of duration that the stress factor persists. Suppressiveness of soils to SBPP and diseases may be considered as an expression of the soil resilience capacity where soil microorganisms multifunctionality must play an important role. Soil resilience is defined as the ability of a soil to recover to its initial state after a stress event [134]. Suppressiveness/resilience may not be necessarily manifested in every soil in natural environments and even less in agroecosystems.

7. Agroecosystems and biodiversity

Agroecosystems are modified ecosystems by man in which plants, animals and microorganisms biodiversity has been altered, and sometimes decreased to a minimum number of species [135, 136]. Agroecosystems are simplified systems at different levels of their structure and function where biological interactions and relationships have been disrupted, and these disturbances are expressed at different levels of organization [136]. There is a great diversity of agroecosystems in the world, from traditional multiple cropping systems under subsistence agriculture established mainly in tropical regions [8] to highly technified and extensive monocropping systems established under intensive agriculture mostly in the temperate regions [137]. Therefore, it is expected that the soil ecosystem biodiversity,

structure, and function be altered at different levels. It is important to consider that the change from a natural ecosystem into an agroecosystem will always bring alterations above- and below-ground regardless of if this is a traditional, or multiple or intensive cropping; most of the different agronomic activities applied (tillage, fallow, herbicides, manure, etc.) in a crop land will certainly cause alterations in the soil ecosystem. But how important will be these changes? Which species and functions will be affected and how this will be manifested in the soil food web structure and functions? Certainly, these are no easy questions to answer. However, if we think about the most important functions of the soil ecosystem performed by the soil biota: organic matter decomposition, nutrient release and cycling, and energy flow (soil food web and *complementary relationships*), we may decide which elements and factors to weigh for a better agroecosystem design and management, affecting as little as possible soil biodiversity and soil food web functions.

The specific agronomic requirements for the crop of interest must also be considered. Intensive and extensive agroecosystems (e.g., cereal crops), are highly uniform in their genetic, physiological, and morphological structure and function [135, 136]; and the different agricultural practices such as tillage, herbicides, sowing, improved seed, fertilizers, and pesticides are usually applied with machinery, which may cause a great disturbance in the soil system. In the other hand, in traditional multiple cropping systems there are crop plants diversity and sometimes also weed diversity, they may resemble more to a nature plant community and therefore soil alterations are expected to be less [8, 135, 136]. Several researches have documented how changes aboveground and belowground affect soil biodiversity, structure and function in agroecosystems; Wardle [138] found there were disturbances on detritus food webs because of applying different tillage (no-tillage, conventional tillage) and weed management practices. Tsiafouli et al. [139] sampled soils from different agronomic management (perennial, intensive and non-intensive) in several European countries with the objective to find out how agricultural intensifications affect soil biodiversity; they found that intensification reduced richness and diversity Shannon index of faunal groups but also the average taxonomic distinctness and average breadth of related species, this mean, agricultural intensifications causes a loss of taxonomic diversity, and in turn, soil functioning maybe affected too.

Plant roots (and some death plant residues) are, as producers, in the first soil trophic level and they are source of energy for the upper trophic levels. Some ecological studies propose productivity as key component for the structure, diversity and stability in a food web [110]. Therefore, when a natural ecosystem is changed to an agroecosystem, we expect a cascade effect that will cause a disruption in plant diversity, plant species abundance and plant community composition and in turn there will be alterations in plant productivity (including root productivity), and this will affect the soil food web diversity, complexity and stability [139].

8. Root pathogens in agroecosystems

Plant diseases and epidemics caused by SBPP in agroecosystems are common, and they cause great economical and crop yield losses [12, 140]; some of them have been well studied and documented e.g., avocado root rot caused by *Phytophthora cinnamomi* [141], *Fusarium oxysporum* wilt diseases in vegetables [142], *Ralstonia solanacearum*, a bacteria, causing vascular wilt diseases in more than 200 host plants [143]. It is important to mention that for a disease to develop there must be a susceptible plant host, a virulent plant pathogen and an environment suited to its growth, these are the three components of the conceptual model “disease triangle”, a key in

Plant Pathology [144]. Plant disease epidemics and therefore soilborne disease outbreaks may occur for an increase in the pathogen populations (inoculum density), by an increase in the host plant susceptibility (age, phenological stage, nutritional status, genetic background) or by certain environmental conditions (biotic and abiotic) conducive to the disease expression, e.g., biologically impoverished soil, deficient water drainage [12, 140]. The degree of root damage or severity is generally related to the number (inoculum density) and type of pathogens, which results in root rot wilting, necrosis, poor growth, and stunted development (deformations), these root alterations impair nutrient and water uptake, affecting in turn development of the whole plant with a decrease in biological and economical crop yield and food quality [114, 117]. Increments in SBPP populations and damages in roots affect development and kind of exudates, which may affect other microbial populations altering in turn soil food webs, in a cascade effect. Management of SBPP and disease outbreak in crops, consider the addition of organic matter, cover crops, green manures, composts, crop rotation, and multicropping as adequate strategies because they decrease pathogen soil inoculum through enhancement of antagonistic relationships, they also improve plant growth and resistance, multiplication of beneficial soil microorganisms, and these strategies also enhance the soil suppressiveness/resilience [7, 145, 146].

9. Management of root pathogens and diseases they cause in agroecosystems

Since an ecological point of view, plant disease epidemics caused by SBPP in agroecosystems are relevant because the different control strategies applied are mainly directed to the soil, trying to decrease pathogen inoculum density and population dynamics [116]. Among these strategies we found: 1) Application of chemical pesticides [147]: fungicides, nematicides, antibiotics, including biocides like Methyl Bromide, which have an evident negative effect to the soil biodiversity. 2) Biological control [148], which involve the introduction in the soil or substrate where plants are growing, specific bacteria or fungi species or strains that function as pathogen antagonists or plant-growth promoters or drivers of the plant host resistance; the effects of this strategy on the soil community function and structure, are not very well known. 3) Plant host resistance [149, 150], obtained through the genetic improvement of the crop species by breeders using traditional breeding techniques or modern genetic engineering methodologies introducing resistance genes into the host crop (genetically modified organisms GMO); the effects of this modified organisms in the soil community and soil food web, are also not well known. 4) Cultural Management [7, 151], like soil quarantine, soil disinfestation, intercropping and crop rotation, tillage, planting date and plant spacing. 5) Management of the soil environment such as mulching, biofumigation, composts, and composts added with pathogen antagonists [7]. Management strategies 4 and 5 have a direct effect and alterations on the soil communities and food web, all these strategies imply application of organic matter into the soil, However, several questions surge: What is the best way to apply it? Is it the right kind of organic matter for a specific SBPP and disease? How long last their effects? How important is the application of organic matter and the introduction of antagonists in the soil community? What groups or species of antagonistic organisms are the most adequate? How will these strategies affect the soil microbial community? How the soil food web will be disrupted? How much these methods affect important soil functions? Until now, there is not enough ecological research about how much soil biodiversity is affected, mainly microbiome diversity, and

therefore soil food web structure and function, as a result of the strategies applied for root pathogens management. Here is interesting to mention work by Wolfgang et al. [152], with tomato crop in Uganda, where they screened from rhizosphere and surrounding soil the different groups of bacteria antagonistic to the root-knot nematode *Meloidogyne* spp. and several root pathogenic fungi, e.g., *Fusarium oxysporum*, *Botrytis cinerea*, *Sclerotium rolfsii* and *Verticillium dahliae*. *Meloidogyne* spp. is a SBPP involved in several complex diseases interacting with other plant pathogens and damaging important vegetable crops like tomato around the world and causing great crop losses. Researchers find out that infection with nematodes was correlated with a strong bacterial community shift in tomato roots, with a microbiome from healthy plants differing from infected roots, and they concluded that the different functions performed by the antagonistic microbes, including volatile organic compounds, all together can lead to synergistic beneficial effects preserving the stability and diversity of macro- and microhabitats. Their results show that rhizosphere and surrounding soil microbes, function in a complementary conjunction, performing multiple roles in a complex and dynamic system. Must be said, that there is need of research on these topics in agroecosystems with a wider view, taking into consideration soil ecological processes and principles.

10. Proposals for SBPP and diseases management, under ecological and sustainable soil biodiversity and conservation

The study and management of plant diseases is now supported for epidemiological concepts and methodologies, which allow to understand the diseases as dynamic spatio-temporal processes at the population and community levels, involving tree main components: the pathogen, the host plant and the environment (biotic and abiotic), forming the 'disease triangle', a key concept in the study of pathosystems [140, 144]. In this way, plant disease epidemiology, specifically temporal and spatial quantitative analysis of the pathosystem, set up the basis for the design of better disease management strategies in both airborne and soilborne pathosystems [12, 140]. However, this epidemiological approach must be enhanced applying ecological concepts, principles and methodologies that enrich and preserve soil diversity and the soil food web structure and functions, applying organic agriculture, composting, crop rotations and green manure [7]. A relevant consideration is to perform epidemiological research in soilborne plant diseases in long-term studies (5–7 years), under a regional (landscape) level [153] with different genetic populations of the pathogen and the host, which allow to find out how their populations are structured and have coevolved, adding another important element for understanding the genetic and evolutionary basis of the diseases, and their relation with the soil microbial community and the soil food web structure and function [13, 154]. Another especially important consideration is about agricultural intensification [155], which Tsiafouli et al. [139] demonstrated that intensification has a consistent negative effect across most soil food web components and that is not limited to specific groups of soil biota; this implies the urgent need to redesign our agroecosystems in such a way to preserve soil biodiversity and the soil ecosystem. At present, an interesting proposal for the SBPP management is the genetic redesigning of beneficial and pathogenic microorganisms of plant, soil, and root rhizosphere, pursuing the development and enhancement of soil suppressiveness and plant host resistance, from the lowest biological organization level [156]. However, several questions arise: Are we taking in consideration the importance of and the transcendental evolutionary and coevolutionary relationships among the species involved in pathosystems, in the soil food webs, in the soil ecosystem? Certainly, SBPP and diseases management

strategies need to be understood following and applying ecological principles, but also evolutionary principles [15, 157].

11. Conclusions

Soil ecosystem is the support for maybe every living on earth; their development and evolution takes thousand and millions of years; however, agroecosystems have caused great changes in soils worldwide, and in many cases soils have been impoverished, run out of nutrients and organic matter, contaminated and even eroded; which means soils biodiversity structure and functions have also been greatly disrupted, and in consequence vital soil functions such as organic matter decomposition and nutrient cycling and release. Plant diseases and disease epidemics caused by SBPP have relevance in soil ecology because most strategies applied for their management are directed to the soil, affecting biological, physical and chemical soil characteristics, and altering soil diversity and soil food webs. However, human societies need to produce enough and healthy food, and soil ecosystem is the source from where to obtain healthy crops; therefore, agroecosystems must be redesigned urgently, based in the knowledge of above- and below-ground communities structure and function, and diversity conservation, to develop a sustainable agriculture with minimal impact of agricultural practices on the environment and taking care of maintaining or improving soil fertility. There is need of an integral interdisciplinary research of SBPP and diseases, considering these pathogens and processes as dynamic components of the soil ecosystem, where the analysis of the soil food webs and complementary interactions be a fundamental aspect for their management, involving epidemiological, ecological, and evolutionary principles and methodology.

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